

# The Evolution of Angiosperm Trees: From Palaeobotany to Genomics

Quentin C.B. Cronk and Félix Forest

**Abstract** Angiosperm trees now rival the largest conifers in height and many species reach over 80 m high. The large tree life form, with extensive secondary xylem, originated with the progymnosperms and gymnosperms in the Devonian and Carboniferous. However evidence suggests that the ancestor of extant angiosperms was not a tree but either a herb or understory shrub. Angiosperm fossil woods are rare in the early Cretaceous but become common in the mid-Cretaceous. The “reinvention” of wood in the Cretaceous produced a novel xylary morphospace that has since been extensively explored by subsequent evolution. Today, large timber trees are absent in the early diverging lineages of the angiosperms, and conventional wood has been lost in the monocots. There are a few timber trees in the magnoliid clade. Most timber trees are in the rosoid clade, particularly the fabids (e.g. Fabaceae) but also in the Malvids (e.g. Meliaceae). Timber trees are less common in the strongly herbaceous asterid clade but some important timbers are also found in this lineage such as teak, *Tectona grandis* (Lamiaceae). Genomic resources for angiosperm trees are developing rapidly and this, coupled with the huge variation in woody habit, make angiosperm trees a highly promising comparative system for understanding wood evolution at the molecular level.

**Keywords** Wood • Fossils • Evolution • Xylogenesis

## Introduction

The tallest known angiosperm tree is “Centurion”, a large *Eucalyptus regnans* from Tasmania measuring 99.6 m in height, 12 m around at the base, with an above ground biomass of 215 tonnes and an annual increment approaching one tonne (Sillett et al. 2015). This is a big tree by any measure. *E. regnans* is only the third

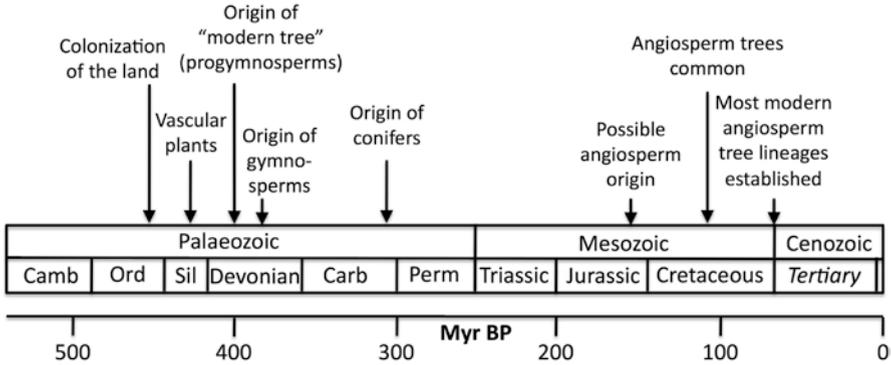
Dr Douglas† is sadly recently deceased.

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© Springer International Publishing AG 2017  
A.T. Groover and Q.C.B. Cronk (eds.), *Comparative and Evolutionary Genomics of Angiosperm Trees*, Plant Genetics and Genomics: Crops and Models,  
DOI 10.1007/7397\_2016\_31



**Fig. 1** Timeline of the evolution of the angiosperm tree habit (see also Table 1)

largest tree species after two conifers, the coast redwood and coastal Douglas<sup>†</sup> fir of western north America. However, a disputed nineteenth century record, at 132.6 m, would make *E. regnans* the world's tallest tree, if correct.

Although conifers hold most of the height records, angiosperms are notable in certain categories. Their capacity for clonal growth means that “Pando”, a large aspen (*Populus tremuloides*) clone is the largest organism by biomass. It is estimated that the Pando clone covers 46.3 hectares (DeWoody et al. 2008). *Ficus benghalensis*, the Indian banyan tree, has the largest spread of a single tree. Descending prop roots stabilize branches which can grow horizontally almost indefinitely. One individual, “Thimmamma Marrimanu”, is said to occupy an area of 1.9 hectares.

It was not always so. It is likely that angiosperms were once small and evolved in the shadow of gymnosperms. They took millions of years to attain ecological dominance over gymnosperms (at least in most forest biomes) and millions more to fully rival the tallest gymnosperms in size. In terms of geological history however, the rise of the angiosperms was spectacularly rapid. This chapter will follow the road to ecological dominance of the angiosperm tree. Tree genomics holds the promise of being able to understand this rise and to understand the genomic toolbox (Schrader et al. 2004; Groover 2005; Carocha et al. 2015) used to build such forest giants. The origins of this toolkit lie in the distant evolutionary past. It is therefore useful to start the journey at the earliest land plants and what genes they brought with them, from their aquatic ancestors, onto the land (Floyd and Bowman 2007), around 470 million years ago (Mya). A timeline of land plant evolution is given in Fig. 1. By comparing genomes of trees with those of the early diverging extant land plants, such as the moss *Physcomitrella patens*, we can determine the conserved developmental modules which have been reshaped, co-opted or re-used, in order to build massive organisms (Xu et al. 2014).

## Early Land Plants and the Building Blocks of Complexity

Increased knowledge of the biology of *Physcomitrella patens* has allowed us a glimpse into what aspects of the molecular machinery of woodiness is shared

with early divergent clades of land plants and may be considered to have involved soon after the colonisation of the land. Three examples can be cited: (1) The KNOX proteins. These are essential for meristems function and are involved in cambial activity (Champagne and Ashton 2001; Singer and Ashton 2007; Sakakibara et al. 2008). (2) The NAC transcription factors. These are essential as regulators of xylogenesis (Xu et al. 2014). (3) The lignin pathway, including genes like 4CL (Silber et al. 2008; Souza et al. 2008). There are many examples of evolution re-using and co-opting existing genes rather than evolving novel genes *de novo*. It is therefore unsurprising that we can find the molecular origins tree-building in distantly related simple plants and infer their presence in the common ancestor of extant land plants.

## Vascularization: The Lignin Revolution

The earliest land plants had no vascular tissue and were unable to transport water for long distances. This constrained their size and ensured dependence on external water: they were ectohydric, with water transport by capillarity along the external surface of the plant.

The endohydric condition (internal water transport) is characteristic of the more robust mosses and therefore predates vascularisation and its precursor. Endohydric mosses can absorb substrate water through basal rhizoids, and are resistant to water loss because of a cuticle-like external layer. In their stems they have well-developed conducting strands or hydroids (Zamski and Trachtenberg 1976). Examples of endohydric mosses include *Polytrichum* spp., and the largest mosses, such as *Dawsonia superba* and *Dendroligotricum dendroides* (Atala and Alfaro 2012). The hydroids together make up a conducting tissue called the hydrome (there is also a phloem-like tissue called leptome). It is debatable whether the hydrome and leptome of mosses are directly homologous to xylem and phloem or whether they represent independent evolution. Nevertheless the early stages of evolution of xylem and phloem must have been equivalent to hydrome and leptome, and therefore we can use those tissues to help us understand vascularisation (Edwards et al. 2003). Hydrome is often particularly well-developed in the sporophytes of mosses, which also have stomata. Stomata therefore predate the origin of xylem but their association with hydrome in sporophytes of mosses indicates the likely co-evolution between conducting tissues and stomata (Ligrone et al. 2012).

Plants with simple patterns of xylem and phloem (primary vasculature) occur in the fossil record (Table 1) with the appearance of the rhyniophytes (Kenrick and Crane 1991) (leafless herbs, now extinct), lycophytes (microphyllous herbs) and ferns (megaphyllous herbs). The lycophytes and ferns also evolved strategies to form tree-like organisms, which will be discussed later, but these are more akin to giant herbs than true trees.

The tracheid, eventually with its lignified cell wall (Boyce et al. 2003), represented a great improvement over the hydroid in terms of water transport and the

existence of xylem (tracheid tissue) permitted water transport over greater distances, thus allowing for greater organismal stature.

The development of primary xylem is a first step in the ontogeny of shoots, even in large extant trees, and there is no reason to suppose that primary vascularization is not fundamentally homologous throughout vascular plants. Unfortunately there are rather few simple vascular plants with completely sequenced genomes. *Selaginella* (a lycophyte) is one (Banks et al. 2011), and there are plans to sequence the model fern, *Ceratopteris richardii* (Veronica Di Stilio, pers. Comm.). Further resources of this sort would be extremely valuable in studying the evolution of vascularisation.

Currently our knowledge of primary vascularisation at the molecular level comes, of course, from *Arabidopsis*. The developmental course involves, first, the differentiation and division of procambial strands (Yang and Wang 2016). Second comes differentiation into protoxylem and protophloem and thirdly the formation of metaxylem and metaphloem. Genes involved in these processes are numerous but include HD-ZIP III genes that direct xylem development. Polar auxin transport (PAT) is very important: auxin mediated transcription of MONOPTEROS (MP) leads to the expression of the HD-ZIP gene AtHB8, as well as the PIN1 auxin transporter which maintains MP transcription in a positive feedback loop (Ohashi-Ito and Fukuda 2010). A key question is how these gene modules of primary vascularization evolved in the early history of life on land (Xu et al. 2014).

## Vascular Elaboration: Trees without Woody Trunks

Woody trunks, as discussed in the next section, are a feature of the progymnosperms, gymnosperms and angiosperms, together forming a single clade the lignophytes. However, tree-like organisms evolved in the lycophytes and ferns, despite less extensive development of secondary vasculature. There are no extant tree-like lycophytes, but in the fossil record of the Carboniferous, *Lepidodendron* and *Sigillaria* grew to tree-like proportions in the coal swamps (Phillips and Dimichele 1992; DiMichele and Bateman 1996). These tree lycophytes had some secondary xylem, produced from a unifacial, and more or less continuous, cambium. However, this secondary xylem did not occupy the bulk of the stem, but only a small central core. The majority of the stem was parenchymatous with structural rigidity provided by a well-developed outer bark. They could almost be described as “giant herbs”, particularly as the arborescent stems were determinate and short lived. The closest living relative to these giant herbs is now the quillwort group, comprising the small aquatic *Isoetes* and its small shrubby relative *Stylites* (Karrfalt and Hunter 1980; Larsen and Rydin 2016). These extant plants would be an exciting genomic resource for the study of the origin of the tree habit in fossil lycophytes. However, no genomic resources are currently available for quillworts.

The tree habit has also evolved in ferns (monilophytes) and indeed we still have extant examples in tree ferns (Pteridophyta), such as *Dicksonia* and *Cyathea*. These

can grow several metres high but have no secondary xylem. Instead they have a complex primary vasculature (dictyostele) in a massive, mainly parenchymatous stem. Much of the structural rigidity of the stem comes from a tough outer layer of persistent leaf-bases or adventitious rootlets. These too have the aspect of a “giant herb”. An extinct group of free-sporing plants, the Cladoxylales, attained considerable stature (Soria and Meyer-Berthaud 2004). The cladoxylalean *Eospermatopteris* (*Wattieza*) has left Devonian fossils in New York State that are massive trunks from organisms formerly 8 m or more high (Stein et al. 2007). Finally, a rather divergent group of ferns (in the broad sense), the horsetails or sphenophytes, are also represented by large organisms in the fossil record. The arborescent sphenophytes produced a small amount of secondary xylem in their long and narrow stems, which grew many metres high (Rossler and Noll 2006; Roessler et al. 2012). The stems are cylinders of wood around a central pith. This is a different strategy but they are still hard to fit into the modern concept of “tree” and again have something of a resemblance to “giant herbs”, particularly as the aerial stems were likely mostly determinate and short-lived.

## The Evolution of Woody Trunks: The Progymnosperm Legacy

The woody trunk or “hyperstele” (massive secondary development of the primary vasculature or stele) evolved first in the progymnosperms. The formation of woody trunks required the extensive production of secondary vascular tissue from a persistent and highly active continuous cambium. This permits massive stems (trunks) that are very largely composed of xylem with little or no pith (although some seed plants do have trunks with extensive pith - see below). The structural strength of such secondarily thickened stems allows for indeterminate growth into very large organisms. This contrasts with the determinate tree-like stems of arborescent lycophytes and horsetails which spring up to considerable heights to reproduce, but might not persist.

The position of the first “modern tree” is generally given to the progymnosperm *Archaeopteris* (Meyer-Berthaud et al. 1999). Progymnosperms do not have seeds but are instead free-sporing, indicating that the woody trunk evolved well before the seed. Progymnosperms appear to have had tracheids with bordered pits (Dannenhoffer and Bonamo 2003). Fossil wood of *Archaeopteris* is commonly referred to in paleontological literature as *Callixylon* (Beck 1960) and studies of well preserved *Callixylon* wood shows not only the presence of bordered pits but also of possible torus structures (Beck et al. 1982). If this interpretation is correct, then *Archaeopteris* shows advanced features of conifer wood. Wood features characteristic of conifers therefore predates conifers and even the seed habit.

When gymnosperms appear in the fossil record, they carry forward the massive wood construction of the progymnosperms (Savidge 2008). Their generally large size, together with the advantage of the seed, gave rise to ecological success. Millions of years of increasing gymnosperm dominance of the earth eventually left

only epiphytic, aquatic, marginal or forest understory niches for lycophytes and ferns. However, not all gymnosperms have the massive trunks of conifers. The solid wood and pith-free trunks of conifers is a form of construction termed “pycnoxylic”, whereas the trunk of cycads is “manoxylic”, with a large pith. *Ginkgo* has a mixed stem anatomy with the short shoots being manoxylic and the long shoots pycnoxylic. The final group of extant gymnosperms, Gnetales, is remarkable for its diverse habits, from lianas to small shrubs, and for the presence of vessels, independently derived from those of angiosperms. This diversity indicates the ability of this lineage to utilize different modes of woodiness in addition to the massive woodiness of conifers.

It is worth noting that this new innovations leading to massive wood partly involve the distribution and number of tracheids and partly changes to functional efficiency the tracheid itself. The basic tracheid building block is little changed from the earliest vascular plants to appear on the land, but some innovations have arisen, such as the bordered pit complete with torus (characteristic of some conifers). Many ferns and lycophytes have undifferentiated pit margins (although bordered pits have been noted in some).

Far more conspicuous, however, is the huge increase in distribution and volume of xylem. The key innovation for this lies in the persistent and continuous cambium. The challenge for genomics and development is therefore in understanding the specification and maintenance of the cambium (Groover and Robischon 2006).

## Wood Reinvention: The Evolution of Angiospermous Wood

The first unequivocal angiosperm fossils are pollen grains that first appear in the early Cretaceous (from 135 Mya). At first rare, angiosperm pollen quickly increases in abundance, first in low latitudes, later in higher latitudes. By the end of the Cretaceous the angiosperms were clearly the dominant organisms of the biosphere. The first macrofossil evidence is *Archaeofructus* (Sun et al. 2002), an aquatic herb from the early Cretaceous (125 Mya). However, molecular dating studies consistently suggest angiosperm origins well before this, usually some time in the Jurassic. The fossil flower *Euanthus* (Liu and Wang 2016), from the late Jurassic (160 Mya) is not universally accepted as an angiosperm. Enigmatic fossils from the Triassic such as the “monocot-like” leaf *Sanmiguelia* and some angiosperm-like triassic fossil pollen (Hochuli and Feist-Burkhardt 2013), hint at an even earlier origin. If angiosperms did originate before the Cretaceous the problem becomes how they remained so rare for so long. Darwin (1903) recognized this problem when he wrote in a letter in 1875: “the presence of even one true angiosperm in the Lower Chalk [early Cretaceous] makes [one] inclined to conjecture that plant[s] of this great division must have been largely developed in some isolated area, whence owing to geographical changes, they at last succeeded in escaping, and spread quickly over the world” (Darwin and Seward 1903).

Features of the first angiosperm may be looked for by examining the early diverging lineages *Amborella*, Nymphaeales and Austrobaileyales (Table 2). There are two growth forms here: *Amborella* and the Austrobaileyales are generally shrubs or lianas adapted to low light and high soil disturbance in humid tropical forest understory, such as stream banks in tall forest. This model of the early angiosperm is the “dark and disturbed” hypothesis (Feild et al. 2004). The Nymphaeales are very different. They are aquatic and adapted to sunny open water. This has led to the suggestion that the early angiosperms might have been aquatic: the “aquatic palaeoherb” hypothesis (Sun et al. 2002; Feild and Arens 2005).

Either way, there is no evidence that the ancestral angiosperm was a tall forest tree. Interestingly, both *Amborella* and the Austrobaileyales have a seedling phase in which they form multiple scandent shoots from a basal lignotuber (Feild and Arens 2005). Sometimes the scandent habit persists as in lianous species of *Schisandra*, *Austrobaileya* and *Trimenia*. This is interesting as the lianous habit is potentially a driver for the evolution of vessels, as may have been the case in *Gnetum* (of which many species are lianous). High hydraulic conductivity per unit area is important in the thin stems of lianas. It should be noted however that lianous species without vessels are known (Feild et al. 2012).

Waterlilies (Nymphaeaceae) have large creeping rhizomes that are often perennial. Despite the large size they have no secondary xylem and do not form a vascular cambium (although there may be a cork cambium). Instead the primary vasculature is scattered and the bulk of the rhizome is of aerenchymatous ground tissue.

Whatever specialized niche, whether understory shrub, liana or aquatic herb that early angiosperms occupied, the ecological conditions were apparently permissive to a distinctive “reinvention” of wood: now with vessels and small bordered pits with a homogeneous pit membrane (lacking a torus). Notably, if the ancestral angiosperm was an aquatic herb then woodiness, and even the vascular cambium (if this was ancestrally lost), might have had to be re-evolved.

Whatever the ecological drivers, when angiosperms increased in numbers and stature in the mid-Cretaceous to compete with gymnosperms in the forest canopy, they possessed a remarkable new vesseliferous wood. There are only a few angiosperms with only tracheids (i.e. vessels completely absent). This feature maybe ancestral in *Amborella* but it is an evolutionary reversal elsewhere (Winteraceae in the magnoliids, and *Trochodendron* in the eudicots). As Feild and Arens state: “vessel origin appears to allow for the exploitation over new morphospace of xylem hydraulic design” (Feild and Arens 2005). This new morphospace has been fully exploited in subsequent angiosperm evolution.

A likely further reinvention of wood occurred in the monocot clade, which appears to have diversified from an herbaceous ancestor. The palms are monocots with an anomalous “wood”, formed from extended production of fibre-capped vascular bundles distributed throughout the ground tissue. Compared to dicotyledon xylogenesis this seems bizarre and it produces “wood” unlike any other. This is not wood if that is defined as secondary xylem, but if wood is defined more generally as usable lumber then the word applies. Palm wood is functionally very effective, sup-

porting tall trees (up to 60 m in the case of the wax palm *Ceroxylon quindiuense*) and producing internationally traded and locally important hard tropical lumbers such as “red palm” lumber from *Cocos nucifera* and “black palm” lumber from *Borassus flabellifer*. The trunk is filled with functioning vascular bundles and there is no heartwood of non-functioning vessel elements. Furthermore the absence of a peripheral cambium reduces vulnerability to fire (Tomlinson 2006). The recent sequencing of the genomes of oil palm (*Elaeis guinaeensis*) (Singh et al. 2013) and date palm (*Phoenix dactylifera*) (Al-Dous et al. 2011; Al-Mssallem et al. 2013) has created opportunities for understanding the distinctive growth of palm trunks at the molecular developmental level.

There are now genomes available or soon-to-be available for several early divergent clades of the angiosperms, notably *Amborella* (Albert et al. 2013). These genomes will be of great significance for comparative work that seeks to elucidate the evolutionary developmental origin of angiosperm wood. Finally, mention should be made of a bizarre rootless aquatic dicot angiosperm, *Ceratophyllum* (Iwamoto et al. 2015), which lacks xylem, even primary xylem. As the xylogenesis pathway has been deleted in this plant, it represents a “natural knockout” experiment, which might one day be attractive to researchers.

## Forest Giants: The Origin of Large Angiospermous Trees

The rapid rise and diversification of the angiosperms during the Cretaceous is well documented from fossil evidence. However much of the early differentiation appears to have been in the form of herbs (Jud 2015) and shrubs (Feild and Arens 2005). Fossil angiosperm wood does not appear until the Aptian and Albian (126–99 Mya) and does not become common until the late Cretaceous (84–65.5 Mya). At the same time, findings of fossil gymnosperm wood fall (Peralta-Medina and Falcon-Lang 2012). Recent fossil flower finds allow the identification of magnoliids as well as early diverging clades of eudicots (Proteales and Buxales) (Doyle 2015). By the end of the Cretaceous (65 Mya) the majority of eudicot lineages were well established and the abundance of fossil woods indicate that large eudicots were dominant in forests globally (Tables 3).

The first diverging extant eudicot lineages include many herbaceous and shrubby clades (Bremer et al. 2009; Group 2016). However, the order Proteales includes the plane trees (*Platanus*), which are of large stature. Extinct platanoids (Maslova 2010) of various kinds may have been among the first eudicot forest dominants.

The delimitation of the eudicot clades used here (Table 3) follows the recent APG classifications (Bremer et al. 2009; Group 2016). The asterid clade of eudicots includes rather few large trees (although many herbs, as in the predominantly herbaceous family Asteraceae). *Gmelina* and *Tectona* (teak) in the mint family Lamiaceae are notable exceptions. By contrast, the rosid clade (containing about a quarter of flowering plants) contains the majority of large trees on the planet

**Table 1** Some major plant lineages mentioned in text

Name	Origin (approx.)	Notes
Liverworts (marchantiophytes)	Mid-Ordovician (470 Mya)	Earliest land plants (mid-Ordovician) are probably referable here; or at least were similar in form to modern marchantiophytes
Mosses (bryophytes)	? Silurian (c. 440 Mya)	Fossil record poor
Hornworts (anthocerotophytes)	? Silurian (c. 435 Mya)	Fossil record poor
Rhyniophytes (extinct)	Mid-Silurian (430 Mya)	The early vascular plant, the rhyniophyte <i>Cooksonia</i> is first known from fossils in Ireland (Edwards and Feehan 1980).
Lycophytes	Late Silurian (420 Mya)	The first fossil evidence is the relatively small lycophyte <i>Baragwanathia</i> from Australia
Ferns (monilophytes)	Likely late Silurian (420 Mya)	The earliest fern (in the broad sense) fossil is generally considered to be the mid-Devonian (c. 390 Mya) <i>Ibyka</i> . (possibly representing a lineage ancestral to sphenopsids) However the fern and lycophyte lineages are likely to have split before this
Progymnosperms (extinct)	Mid Devonian (c. 400 Mya)	The mid-Devonian Aneurophytales are the first exemplars. The first “modern tree”, <i>Archaeopteris</i> , first appears in the upper Devonian (380 Mya)
Gymnosperms	Late Devonian (385 Mya)	The first gymnosperms are not referable to any extant groups. The first members of extant groups, such as the first putative conifers, arose in the late Carboniferous (310 Mya)
Angiosperms	Possibly late Jurassic (160 Mya)	Unequivocal angiosperm pollen first appears in the early Cretaceous (from 135 Mya). The fossil flower <i>Euanthus</i> (Liu and Wang 2016), if accepted as angiospermous, pushes the origin back at least to the late Jurassic (160 Mya)

**Table 2** Characters of the major clades of angiosperms

Clade	Life form	Xylem characters
<i>Amborella</i>	Shrub	Extensive bifacial vascular cambium, tracheids only
Nymphaeales	Aquatic herbs	Primary xylem only, vessels
Austrobaileyales	Shrubs, lianas	Extensive bifacial vascular cambium, vessels
Magnoliids	Shrubs, trees, lianas, herbs	Extensive bifacial vascular cambium, vessels (but tracheids in Winteraceae)
Monocots	Herbs (rarely trees, e.g. palms)	Primary xylem only (but sometimes with anomalous secondary xylogenesis, e.g. palms), vessels
Eudicots	Herbs, shrubs, lianas, trees	Extensive bifacial vascular cambium, vessels (but tracheids in <i>Trochodendron</i> and <i>Tetracentron</i> )

In addition the Chloranthaceae (a small clade of tropical shrubs of uncertain placement but near magnoliids) has characters of magnoliids. *Ceratophyllum*, an anomalous aquatic genus, has no vasculature

**Table 3** Major clades of Eudicots

Group	Approx. date of origin of extant group	Tree examples
Basal eudicots	132.5–112.9	<i>Platanus</i> (Platanaceae)
Asterids	87.5	<i>Tectona</i> (Lamiaceae)
Rosids	108.7	
Rosid (fabid clade)	98.5	<i>Quercus</i> (Fagaceae), <i>Populus</i> (Salicaceae)
Rosid (malvid clade)	100.5	<i>Eucalyptus</i> (Myrtaceae), <i>Acer</i> (Sapindaceae)

Dates follow recent fossil-calibrated molecular dating studies (Magallon et al. 2013, 2015)

(Wang et al. 2009). It may be divided into two groups: the fabids (the richest clade of large angiosperm trees) and the malvids. The fabids include poplar and oak among many other timbers, while the malvids contain eucalyptus and maple (see Table 4). The fabid order Malpighiales (the order that includes the largely tropical families Salicaceae and Euphorbiaceae) has diversified strongly as small trees in the tropical forest understory (Davis et al. 2005). The initial diversification of this clade (estimated in the mid-Cretaceous) has therefore been taken as a marker of the closure of the canopy of a newly angiosperm-dominated wet tropical forest (Davis et al. 2005).

The distribution of large timber trees is far from random. Figure 2 shows all the families of flowering plants with at least one species of commercial timber (Mark et al. 2014) mapped on (inner circle). The outer circle shows the distribution of the most important timber families (i.e. reported as having at least three major timber species). The concentration in the rosid clade can be readily seen (see legend to Fig. 2).

The evolution of the rosid clade enabled the dominance of angiosperms in forest ecosystems. Within the rosids, the tree morphospace has been extensively explored over the last 100 million years. The range of tree architecture and growth characteristics is staggering: from fat trunks like baobabs (*Adansonia*) to the slender growth of *Trema*; from the huge leaves of *Cecropia* to the small sclerophyllous leaves of *Myrtus*; from slow-growing oaks to fast growing poplars. The multitude of strategies in pursuit of size make angiosperm trees very promising subjects for comparative study.

**Table 4** Important timber families

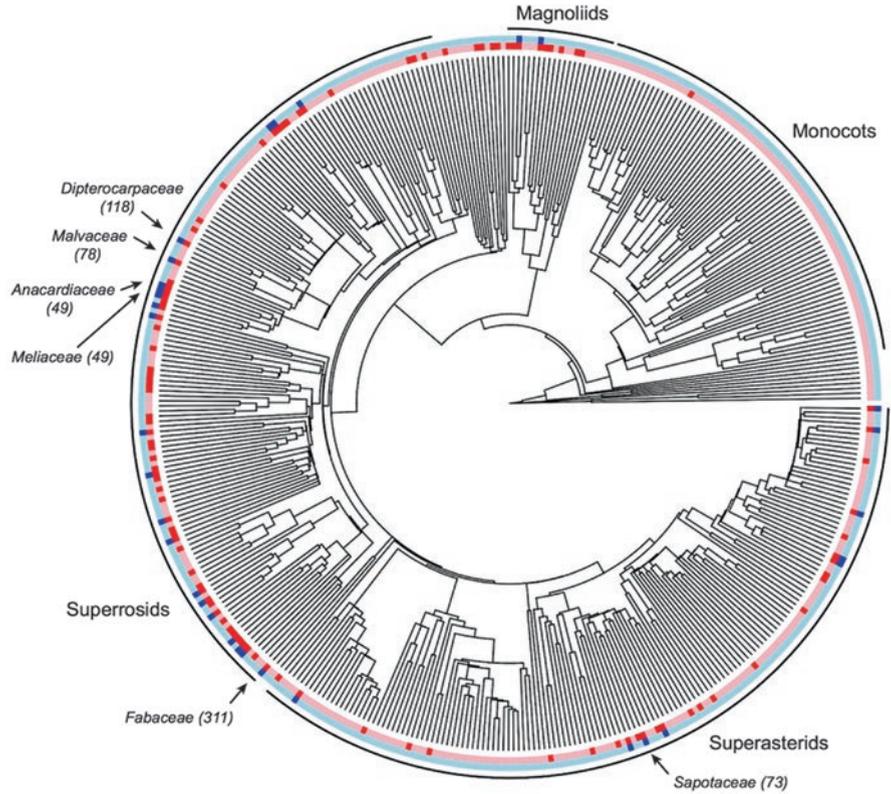
Family	No. of species in family with >5 sources	Order	Group	Sub-group	Example genera (genera with temperate species in bold)
Leguminosae	89	Fabales	Rosidae	Fabidae	<i>Millettia</i> , <i>Dalbergia</i> , <i>Hymenaea</i>
Fagaceae	12	Fagales	Rosidae	Fabidae	<b><i>Castanea</i></b> , <b><i>Fagus</i></b> , <b><i>Quercus</i></b>
Moraceae	9	Rosales	Rosidae	Fabidae	<i>Bagassa</i> , <i>Milicia</i> , <i>Antiaris</i>
Betulaceae	8	Fagales	Rosidae	Fabidae	<b><i>Alnus</i></b> , <b><i>Betula</i></b> , <b><i>Carpinus</i></b>
Juglandaceae	7	Fagales	Rosidae	Fabidae	<b><i>Juglans</i></b> , <b><i>Carya</i></b> , <i>Engelhardia</i>
Ulmaceae	6	Rosales	Rosidae	Fabidae	<b><i>Ulmus</i></b> , <i>Phyllostylon</i> , <b><i>Zelkova</i></b>
Salicaceae	5	Malpighiales	Rosidae	Fabidae	<b><i>Populus</i></b> , <i>Casearia</i> , <b><i>Salix</i></b>
Clusiaceae	4	Malpighiales	Rosidae	Fabidae	<i>Calophyllum</i> , <i>Symphonia</i> , <i>Garcinia</i>
Zygophyllaceae	4	Zygophyllales	Rosidae	Fabidae	<i>Guaiacum</i> , <i>Bulnesia</i>
Euphorbiaceae	3	Malpighiales	Rosidae	Fabidae	<i>Hevea</i> , <i>Endospermum</i> , <i>Hura</i>
Irvingiaceae	3	Malpighiales	Rosidae	Fabidae	<i>Irvingia</i> , <i>Klainedoxa</i>
Rosaceae	3	Rosales	Rosidae	Fabidae	<b><i>Prunus</i></b> , <b><i>Malus</i></b> , <b><i>Pyrus</i></b>
Meliaceae	23	Sapindales	Rosidae	Malvidae	<i>Swietenia</i> , <i>Entandrophragma</i> , <i>Khaya</i>
Dipterocarpaceae	17	Malvales	Rosidae	Malvidae	<i>Shorea</i> , <i>Dipterocarpus</i> , <i>Dryobalanops</i>
Malvaceae	16	Malvales	Rosidae	Malvidae	<i>Ochroma</i> , <i>Tarrietia</i> , <i>Triplochiton</i> , <i>Ceiba</i>
Anacardiaceae	9	Sapindales	Rosidae	Malvidae	<i>Mangifera</i> , <i>Astronium</i> , <i>Camposperma</i>
Myrtaceae	7	Myrtales	Rosidae	Malvidae	<b><i>Eucalyptus</i></b> , <i>Melaleuca</i>
Sapindaceae	7	Sapindales	Rosidae	Malvidae	<b><i>Acer</i></b> , <b><i>Aesculus</i></b> , <i>Allophylus</i>
Combretaceae	4	Myrtales	Rosidae	Malvidae	<i>Terminalia</i>
Rutaceae	3	Sapindales	Rosidae	Malvidae	<i>Eucylophora</i> , <i>Balfouriodendron</i> , <i>Chloroxylon</i>
Vochysiaceae	3	Myrtales	Rosidae	Malvidae	<i>Erismia</i> , <i>Qualea</i>
Sapotaceae	9	Ericales	Asteridae		<i>Tieghemella</i> , <i>Mamilikara</i> , <i>Baitlonella</i>

(continued)

Table 4 (continued)

Family	No. of species in family with >5 sources	Order	Group	Sub-group	Example genera (genera with temperate species in bold)
Rubiaceae	6	Gentianales	Asteridae		<i>Fleroya</i> , <i>Nauclea</i> , <i>Neolamarckia</i>
Apocynaceae	5	Gentianales	Asteridae		<i>Dyera</i> , <i>Aspidosperma</i> , <i>Gonioma</i>
Bignoniaceae	4	Lamiales	Asteridae		<i>Handroanthus</i> , <i>Jacaranda</i> , <i>Roseodendron</i>
Ebenaceae	4	Ericales	Asteridae		<i>Diospyros</i>
Oleaceae	4	Lamiales	Asteridae		<b><i>Fraxinus</i></b>
Lamiaceae	3	Lamiales	Asteridae		<i>Tectona</i> , <i>Gmelina</i> , <i>Vitex</i>
Lecythidaceae	3	Ericales	Asteridae		<i>Bertholletia</i> , <i>Cariniana</i> , <i>Couratari</i>
Olacaceae	3	Santalales	Asteridae		<i>Scorodocarpus</i> , <i>Minquartia</i> , <i>Ongokea</i>
Lauraceae	8	Laurales	Magnoliid		<i>Chlorocardium</i> , <i>Ocotea</i> , <i>Eusideroxylon</i>
Myristicaceae	4	Magnoliales	Magnoliid		<i>Pycnanthus</i> , <i>Virola</i> , <i>Staudtia</i>

Families with at least three examples of well-known timbers (i.e. mentioned in at least five sources in Mark et al. 2014)



**Fig. 2** Phylogenetic distribution of traded timber. Phylogenetic tree of the angiosperms (Qian and Zhang 2014) with inner ring (red) shows families with at least one species used as timber in trade according to a standard list (Mark et al. 2014). Timber species are defined as species reported as having traded timber by two or more of 17 sources. The outer ring shows important timber families (families with at least three timber species reported by five or more sources) in blue. The top six families in terms of number of species used as timber are indicated. Note that there are very few timber species in early divergent angiosperms and monocots. Asterids too have relatively few timber bearing families. Most timber species are in the Rosid clade

**Acknowledgements** We thank Drs. Wm. Stein, Richard Bateman and Paula Rudall for helpful discussion and advice. Work in the laboratory of QC is funded by Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grants Program (grant no. RGPIN-2014-05820).

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